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4 **Demographic uniformitarianism: the theoretical basis of prehistoric demographic research
5 and its cross-disciplinary challenges**

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12
13 **Abstract**

14 *A principle of demographic uniformitarianism underpins all research into prehistoric demography*
15 *(palaeodemography). This principle—which argues for continuity in the evolved mechanisms*
16 *underlying modern human demographic processes and their response to environmental stimuli*
17 *between past and present— provides the cross-disciplinary basis for palaeodemographic*
18 *reconstruction and analysis. Prompted by the recent growth and interest in the field of prehistoric*
19 *demography, this paper reviews the principle of demographic uniformitarianism, evaluates how it*
20 *relates to two key debates in palaeodemographic research and seeks to delimit its range of*
21 *applicability to past human and hominin populations.*

22
23 **Keywords:** Prehistoric demography; Uniformitarianism; Population dynamics; Life History; Archaic
24 hominins

25 **1. Introduction**

26 Like many historical sciences, prehistoric demography relies on a doctrine of uniformitarianism for
27 some of its foundational principles. Uniformitarianism is the adherence to the axiom that processes
28 that occurred in the past (and so cannot be directly experienced) were nonetheless likely to
29 resemble those that are observable in the present day. The utility of a principle of uniformitarianism
30 in prehistoric demography is clear when one considers the database available from which to study
31 the demography of past non-literate societies (palaeodemography). Data derive from a wide range
32 of disciplines but are frequently sparse and inform on a limited selection of demographic parameters
33 [1-5]. Furthermore, these data provide only proxy measures of the demographic variables of
34 interest. Multiple inferential stages are required to turn the data into meaningful statements about
35 prehistoric demography and issues of equifinality abound. A clear underlying theoretical framework,
36 such as that provided by a uniformitarian principle, aids in the reconstruction of prehistoric

37 demographic patterns, providing clear constraints on interpretations of past demographic trends
38 and processes, and justifying the use of estimates for population characteristics and model
39 parameters derived from recent populations to supplement the sparse prehistoric demographic
40 database.

41 Despite providing the basis for all prehistoric demographic research, sustained discussion of
42 demographic uniformitarianism is rare outside of the sub-field of skeletal palaeodemography. As the
43 field of prehistoric demography grows, so does the necessity to ensure that the field's underpinning
44 theoretical basis—and the impact this has on the generation, analysis, and interpretation of
45 prehistoric demographic data—is clear and secure.

46

47 **2. Defining demographic uniformitarianism**

48 The uniformitarian principle was first articulated by geologists in their efforts to understand the
49 mechanisms responsible for the formation of the Earth. As utilised in the historical sciences, the
50 principle argues that there is continuity between processes and causative mechanisms that occurred
51 in the past and those that are observable in the present. There are clear links between
52 uniformitarianism and other heuristic principles of philosophical and scientific argument, such as
53 Occam's razor (the law of parsimony) and analogical reasoning (comparisons that use similarities
54 between independent systems as evidence for the existence of hidden causative commonalities:
55 **Figure 1**). Uniformitarian principles were utilised during the development of demography as a
56 science during the 19th century, underpinning theories of the drivers of, and constraints on,
57 population growth rates **[7]** and large-scale patterns of migration **[8]**. More recently, the argument
58 that demographic parameters derived from historical records of human populations can be used as
59 guidelines for constraining demographic models of prehistoric communities was expressed forcefully
60 by Howell **[9]**.

61 **[Figure 1 near here]**

62 Howell argued that model life tables and fertility schedules—which are constructed on the principle
63 that patterns of age-specific variation in mortality and fertility vary in biologically constrained ways
64 across different populations—could be used to interpolate and smooth fertility and mortality data
65 obtained for prehistoric populations. Howell's uniformitarian assumption was that prehistoric
66 populations occupied essentially the same demographic parameter space observed amongst
67 historically documented populations. She cited Simpson **[10]** and other authorities in support of the
68 argument that demographic aspects of human life histories, including fertility span and longevity,
69 were evolved species-wide attributes. Howell also pointed out that the application of

70 uniformitarianism enables the prediction of otherwise unobservable population characteristics, such
71 as family size and kinship structure, with implications for the role of cultural transmission.
72 Accordingly, the principle of uniformitarianism may also inform on the social, as well as the
73 biological, elements of past demography. However, as Howell makes clear, demographic
74 uniformitarianism does not assume that demographic behaviours have remained the same
75 throughout history but that the basic biological processes relating to fertility and mortality are
76 similar, that they respond to variations in the social and natural environment in the same way, and
77 that these similarities act as constraints and impose limits on demographic behaviours.

78 **3. Uniformitarianism in prehistoric demographic research: two key debates**

79 The implications of the uniformitarian assumption vary depending on the demographic parameter
80 addressed and the palaeodemographic proxy used. Below, we discuss the implications of the
81 uniformitarian principle for two key debates in palaeodemographic research.

82 *a. Population dynamics and the “Forager Population Paradox”*

83 It has long been recognised that there is a stark contrast between the observed population growth
84 rates of recent hunter-gatherers (mean of ~1% per annum [11]) and long-term prehistoric growth
85 rates estimated via palaeodemographic methods which are typically close to zero for foraging
86 populations [12-13]. Explaining this discrepancy (the “forager population paradox” [14]) by
87 presuming that current hunter-gatherer population growth rates are unrepresentative of the past
88 violates the uniformitarian assumption, as long-term population stationarity is only possible via a
89 combined fertility and mortality schedule outside of, or at the extreme limit of, the known range of
90 human variation [12-14]. A more convincing solution is that long term population growth followed a
91 ‘saw-tooth’ pattern, with brief crashes followed by longer periods of recovery [15-16]; a pattern
92 supported by genetic data indicating multiple instances of sharp reductions in prehistoric population
93 sizes (e.g. [17]). In a foraging population with a typical 1% per annum growth rate, the time for
94 recovery from a catastrophic episode causing 50% mortality is only 70 years. Even higher growth
95 rates of up to 3% per annum, and consequent shorter recovery times, have been reported for post-
96 catastrophe indigenous populations in South America, although these high growth rates may be
97 partially accounted for by immigration and group fusion [18]. Such rapid recovery times are too
98 short to be visible by any palaeodemographic method, including the comparatively high-resolution
99 method of summed posterior probability distributions of sets of radiocarbon dates (SPDs) [19, 20]. A
100 difference in scale, rather than in demographic regimes, best explains the discrepancy between past
101 and present embodied in the forager population paradox.

102 What are the implications of this for the reconstruction of prehistoric population growth rates? The
103 uniformitarian assumption relates primarily to underlying mechanisms, not specific parameter
104 values derived from recently observed populations (although the former heavily constrains the
105 latter). Due to the imprecision of radiometric dating, growth rates calculated from
106 palaeodemographic data record only the longer term and slower time-averaged rate across crash
107 and recovery cycles. They are therefore not directly comparable to growth rates recorded in
108 ethnographic and historical contexts which represent 'instantaneous' per annum measures along
109 this continuum of growth and decline. While the uniformitarian assumption likely holds in most
110 prehistoric contexts, this difference in scale means that caution is required when using ethnographic
111 data to interpret models of prehistoric demography, and does not support the simple transference
112 of growth rates from ethnographic to prehistoric contexts; growth rates recorded for recent foragers
113 are not realistic long-term estimates for either the population from which they derive or past
114 hunter-gatherers. Tallavaara [21] further argues that population dynamics derived from
115 palaeodemographic proxies can only be directly interpreted in terms of what controls the long-term
116 mean population size. In the case of prehistoric hunter-gatherers, the primary population limiting
117 factor would be the density-independent variable of environmental productivity [21] leading to
118 debate as to how to combine palaeodemographic results with shorter-term density-dependent
119 growth models derived from population ecology [22], as well as how to infer underlying fertility and
120 mortality rates [23].

121 *b. Age structure of mortality and fertility and longevity in prehistory*

122 Under natural living conditions human populations exhibit regular patterns of age-specific fertility
123 and mortality rates that are strongly age-structured and are likely to be evolved versions of patterns
124 that are common to the great apes [24, 25]. Female age-specific fertility rates follow a unimodal
125 peaked distribution between maternal ages of 15 and 50 years, with peak fertility rates being higher
126 and occurring earlier in farming populations than in foraging populations [26]. The distribution of
127 the risk of death in human populations is bimodal with peak mortality rates in the first year of life,
128 declining to a minimum in adolescence and early adulthood before rising exponentially in later
129 adulthood. These three additive components of human age-specific mortality rates (i.e. juvenile,
130 adult and an age-independent constant risk of death) are represented well by the Siler model [27].
131 Variation in the overall risk of mortality, together with variation in the relative contributions of
132 juvenile versus adult mortality risks, underlie much of the populational variation in attritional
133 mortality that is captured by model life tables.

134 The reconstruction of patterns of mortality and fertility for prehistoric populations is challenging.
135 Fertility leaves few visible traces on the skeleton but can be measured indirectly through its effects
136 on the age distribution of mortality: the latter is constrained by the age distribution of the living
137 population, which in turn is highly sensitive to changes in fertility [28-30]. The variation of mortality
138 risk with age can be inferred from representative samples of human skeletal remains, subject to
139 assumptions about the stability of the age structure of the living population and its average rate of
140 growth. Although survivorship declines with age, the exponential rise in the risk of death at older
141 ages should result in the elderly being well represented in skeletal assemblages. However, when
142 ages at death are estimated for samples of skeletal remains using traditional osteological age
143 indicators, the resulting distribution of age often appears to show an excess of individuals in the
144 young and middle age categories and a corresponding marked deficit of individuals aged above 60
145 years. This abnormal pattern deviates from the strongly age-structured pattern of human mortality
146 described above; it is neither observed in data from model life tables, nor apparent in demographic
147 data from extant foraging and subsistence farming populations, and at face-value implies the
148 inapplicability of the uniformitarian assumption to all prehistoric contexts [31].

149 This common deviation of prehistoric age-at-death distributions from uniformitarian expectations
150 has long been recognised as the likely result of unrepresentative skeletal samples (the result of
151 selective burial and/or differential preservation) and biases in many osteological age estimation
152 methods that affect particularly the oldest age categories [26, 32-34]. Some of these biases stem
153 from identified methodological problems, for example the prediction of age from calibrations
154 against biased reference samples or the use of point age estimates rather than posterior probability
155 distributions. Another potential source of departure from the age distributions predicted by model
156 life tables could arise from the contribution of catastrophic mortality, which elevates the risk of
157 death across all age categories: as young adults comprise a large segment of the living population,
158 they tend to be over-represented in catastrophic death assemblages. For these reasons,
159 considerable caution needs to be exercised when interpreting age distributions estimated from
160 human skeletal remains.

161 Furthermore, regardless of overall levels of mortality, all censused human populations contain a
162 proportion of individuals who live to advanced ages, providing evidence for the evolution of delayed
163 senescence and hence increased longevity in humans as part of the distinctive slow *Homo sapiens*
164 life history pattern. Thus, the underrepresentation of older people in prehistoric skeletal
165 assemblages is problematic not only for accurate reconstruction of the age-specific risk of death, but
166 also for understanding longevity in past populations. Above, we argued that the apparent deficit of

167 older people in the skeletal populations of prehistoric *Homo sapiens* is best explained by biases in
168 preservation and methodological limitations of palaeodemographic analysis. We now return to the
169 key point that demographic uniformitarianism argues for continuity in the evolved mechanisms
170 underlying human demographic processes and pose the question as to why a longer life span was
171 selected for among *Homo sapiens*.

172 Importantly, selection for a longer lifespan has implications for fertility as well as mortality.
173 Cessation of reproduction in females long before the end of life is highly unusual in mammals [35],
174 and a long post-reproductive lifespan is one of the life history traits that distinguishes modern
175 humans from all other primate species. In non-human primates, as is the case in nearly all
176 mammalian species, the approach to maximal lifespan and an irreversible decline in female fertility
177 occur in tandem. In humans, the relative invariance in the timing of menopause, observed both
178 across living human populations and throughout the historical record, together with the lack of
179 evidence for recent secular trends in age at menopause, suggest that humans have retained a
180 hominoid pattern of fertility. The menopause is therefore more likely to be a consequence of
181 selection for longer lifespan, rather than of selection for a shorter reproductive span [36]. Due to
182 their later physiological maturation, human females start giving birth about 5 years later than great
183 apes [37] although with shorter birth intervals in humans even foraging populations achieve higher
184 total fertility than do great apes.

185 One argument is that selection for a longer lifespan enabled older generations, especially post-
186 reproductive females, to enhance the survival chances of their offspring and descendants. This
187 “grandmother hypothesis” is shorthand for a range of evolutionary scenarios that explain the
188 evolution of long post-reproductive lifespans through the selective advantage conferred by
189 grandmothers to their kin - essentially by providing surplus resources to daughters of reproductive
190 age [38, 39]. The extension of post-reproductive female lifespan predicted by the grandmother
191 hypothesis is effectively equivalent to the length of a generation (around 25 years in modern
192 humans) because the fitness benefits conferred by the grandmother diminish sharply when the
193 grandmother’s own offspring terminate their reproduction [40]. When in human evolution did this
194 occur? The pattern of female fertility in modern humans described above appears remarkably
195 plesiomorphic, broadly resembling the ancestral hominoid condition in its age distribution, though
196 with the ability to achieve higher total fertility through maintaining shorter inter-birth intervals. We
197 infer that the modern human pattern of female fertility may also have characterised earlier species
198 in the *Homo* lineage. O’Connell et al. [38] associated the extension of lifespan required by the
199 grandmother hypothesis with the evolution of *H. erectus*/*H. ergaster*, in particular correlating

200 extended longevity with this species' larger brain and body size, and its delayed maturity compared
201 to *Australopithecus*. One prediction from this hypothesis is that the abbreviated hominin lifespans
202 calculated from skeletal data for Middle Pleistocene hominins (*H. heidelbergensis* and *H.*
203 *neanderthalensis* – see below) are likely to be incorrect.

204 **4. Prehistoric demography in the absence of the uniformitarian assumption: the** 205 **palaeodemography of archaic hominins**

206 Howell [9] explicitly excluded non-*Homo sapiens* in her argument for human demographic
207 uniformitarianism. However, the archaeological and palaeoanthropological records of the genus
208 *Homo* extend millennia beyond the initial appearance of *Homo sapiens* in most regions of Africa,
209 Europe, and Asia, and these populations are the subject of a growing body of cross-disciplinary
210 palaeodemographic research [41-47]. The anatomical and behavioural contrasts between all archaic
211 forms of *Homo* on the one hand, and *Homo sapiens* on the other, indicate wider biological
212 differences which render the assumption of demographic uniformitarianism in its strictest form
213 problematic for these populations. This conclusion leads to two further questions which lack easy
214 answers: 1) what is the extent of these biological differences, and how do they relate to the key
215 demographic variables of fertility and mortality? 2) what are the implications of these biological and
216 demographic differences for cross-disciplinary research into the palaeodemography of archaic
217 hominins?

218 The answer to the first question usually begins by seeking to establish when the 'modern human'
219 (i.e. *Homo sapiens*) life history pattern emerged. The life history of extinct hominins is inferred from
220 indirect proxies related to rates of maturation and longevity (body mass, brain size, and dental
221 development) [48-49]. At a minimum, we can state that the modern human life history pattern
222 emerged within the *Homo* clade [50]. However, accurate measurement of archaic hominin life
223 history variables is complicated by fragmentary and small fossil sample(s) and the evidence is often
224 conflicting [51-52]. This is the case even for the archaic hominins of the Middle and Late Pleistocene
225 for whom comparatively large and well-preserved fossil collections exist. For example, comparative
226 analysis of body size, brain size, and dental development indicates that the life history of
227 Neanderthals (*Homo neanderthalensis*) was consistent with that of *Homo sapiens* [49]; a finding
228 supported by a recent study of the growth pattern of the El Sidrón Neanderthal child [53]. However,
229 other studies have suggested a Neanderthal developmental rate both faster [54-56] and potentially
230 slower [57] than those of *Homo sapiens*. While on balance, the data suggest that later archaic
231 hominins (*H. heidelbergensis*, *H. neanderthalensis*) probably had a pace of development within the
232 *Homo sapiens* range, there were likely nonetheless subtle differences related to other aspects of
233 their physiology [53, 58-59].

234 The implications of these biological and life history differences for method and theory in prehistoric
235 demography have been most firmly addressed by practitioners of the skeletal palaeodemography of
236 archaic hominins. As is the case in later prehistory, age-at-death distributions of site-specific and
237 pooled skeletal samples typically do not conform to expectations of age-specific attritional mortality
238 distributions derived from recent populations [42, 46, 60-62]. As shown in section 3b, where the
239 demographic uniformitarian assumption holds we can, with reasonable confidence, interpret this
240 pattern in terms of unrepresentative sampling and inaccuracies in age estimation. However, in the
241 absence of the uniformitarian assumption, no such cross-checks hold, leading to some fierce debates
242 as how to interpret these palaeodemographic profiles.

243 The age-at-death distribution of the Middle Pleistocene pre-Neanderthal hominin fossils from the
244 site of Sima de los Huesos (SH) (Burgos, Spain) is an excellent case in point. These SH hominins all
245 derive from the same lithostratigraphic unit at the site and their taphonomic condition is relatively
246 homogenous, suggesting that they belong to the same biological population [63]. However, the
247 assemblage produces a mortality profile with almost no infants and children, a preponderance of
248 adolescents and young adults, and very few older adults (35 years +) (Figure 2). Wolpoff and Caspari
249 [62] propose that this distribution reflects an attritional profile consistent with the life history and
250 survivorship rates of Middle Pleistocene hominins; an interpretation that they also apply to the age-
251 at-death distribution of the later Krapina Neanderthals from Croatia. Life history data from the SH
252 hominins provides mixed support for this scenario. The pattern and timing of dental development of
253 the SH hominins falls within the range of variation of *Homo sapiens* [64]. On the other hand,
254 calculations of the rate of wear of the anterior teeth (incisors and canines) indicate that these would
255 have been completely worn down by the age of 50 and may have been an important limiting factor
256 on their potential longevity (maximum life expectancy) [65].

257 **[Figure 2 near here]**

258 Nonetheless, as is the case with the age-at-death distributions of prehistoric *Homo sapiens*, the Sima
259 de los Huesos profile is unlikely to be an accurate reflection of demographic reality. Ages of the
260 juvenile hominins in the SH assemblage were undertaken using modern human standards for dental
261 development, which as previously mentioned, probably overlap with dental development schedules
262 for *H. neanderthalensis* and *H. heidelbergensis*. However, the ages of the adult individuals were
263 estimated using the Miles method, which produces a calibration of the amount of dental wear in
264 adults based on the wear rates observed in the juvenile component of the assemblage. As with
265 other skeletal age estimation methods, the Miles method requires adjustment to avoid the under-
266 estimation of age at death in older adults [66], so the estimated ages of some of the adult SH

267 individuals may be too low. The likely presence of much older adults in the SH assemblage is further
268 suggested by the state of the articular surfaces on the SH pelvis 1 specimen [67]. Although the age at
269 death of the SH1 specimen was estimated to fall in the open-ended age category of >45 years,
270 unbiased age estimations based on uniform priors developed for modern human populations (e.g.
271 [68] would suggest a median estimated age for this specimen of between 60 and 70 years. It is
272 furthermore highly likely that the potential for a longer life span was present before many
273 individuals regularly reached it [48], and small skeletal samples are unlikely to include the
274 necessarily outlying individuals who died at extremely old ages [69]. In the case of the SH hominins,
275 arguments for a maximum life span of ~50 years are further weakened by the predicted life spans of
276 *H. habilis* (52-56 years) and *H. erectus* (60-63 years) [70], derived from the allometric relationship
277 between body size, brain size, and longevity among mammals [71].

278 Sampling may also be an important factor in the age-at-death distribution of the SH hominins. The
279 assemblage does not neatly correspond to either an attritional or a catastrophic profile ([61 cf. 62]),
280 but a scenario whereby a catastrophic event impacted a subset of the population is plausible (an
281 exploratory hunting party of young, mobile individuals separated from their larger group; [60, 72]),
282 and instances of catastrophic mortality may have been more common in early population history
283 than usually suspected [26]. The role of biological differences between the early members of the
284 Neanderthal clade at Sima de los Huesos and the modern-day *Homo sapiens* from whom our
285 palaeodemographic models and methods derive should not, however, be excluded from
286 interpretation. Even minor differences in rates of development between archaic hominins and *Homo*
287 *sapiens* —compounded by differences in diet, health and economic conditions [73] —could impact
288 estimates of age-at-death (albeit not the relative distribution of individuals across categories).

289 In other branches of the palaeodemography of archaic hominins, the methodological and theoretical
290 implications of the absence of the uniformitarian principle are less keenly felt but are nonetheless
291 highly relevant. In archaeological demography, the applicability of methods and standards
292 developed from the study of ethnographic and historical populations to pre-modern (i.e. pre-*Homo*
293 *sapiens*) hominins has long been questioned (e.g. [74]). The impact of life history differences on
294 demographic reconstructions and interpretations based on these data —which are primarily used to
295 study changes in relative population size and growth [3-5]—are, however, indirect and hard to take
296 into account, despite both these variables being determined by underlying fertility and mortality
297 rates. Within this branch of prehistoric demographic research, other biological differences between
298 archaic hominins and *Homo sapiens* have a greater impact. The large body mass, and resultant high
299 energy demands of Neanderthals, for example, is a particularly important biological difference

300 between them and *Homo sapiens* [75-76]. High energy requirements and the challenges of obtaining
301 enough food to meet these, particularly in the lack of evidence for food storage, are often cited as
302 potential restrictions on the maximum size of Neanderthal living-groups [77-78], fertility rates, and
303 local population densities [79], and would need to be taken into account in palaeoecological
304 estimates of potential environmental carrying capacity. Within environmental carrying capacity
305 models, the key implication of the higher energetic requirements of Neanderthals is that if foraging
306 from a central place, the effective foraging radius (the area at a distance from camp at which the
307 required amount of energy is equal or more than the net return) would have been smaller than for
308 *Homo sapiens*, meaning that Neanderthal groups would have depleted local resources more quickly
309 and needed to move camp more frequently [78]. This higher mobility—which has a key biological
310 component— also complicates estimates of relative change in population size based on
311 archaeological site counts (e.g. [80]) raising questions about the exact relationship between site
312 quantities and population size (a relationship that is often assumed to be linear, but is in reality
313 unknown), and the possible differences in this relationship between different hominins. More
314 broadly, life history differences, combined with other wider biological and cognitive differences
315 (such as body size, energy expenditure, and brain size) would also have had important implications
316 for population structure, living group size and composition, with attendant repercussions for the
317 emergence of key human social behaviours such as alloparenting, division of labour, and
318 intergenerational cooperation [81]. Dennell [82] posits an important role of these biological
319 differences in the pattern and speed of migration and colonisation of new environments of *Homo*
320 *erectus* and *Homo sapiens* during the Out of Africa 1 and 2 events respectively.

321 **5. Conclusion: challenges and lessons for the use of the uniformitarian principle in cross-** 322 **disciplinary prehistoric demography**

323 The assumption of demographic uniformitarianism is a core principle in palaeodemography. This
324 assumption provides the basic framework for palaeodemographic research across a range of
325 disciplines, allowing for the construction of theoretically plausible models and parameters against
326 which to test and examine palaeodemographic data, and providing the justification for the use of
327 data from ethnographic and historical populations to supplement sparse prehistoric records.

328 The principle of demographic uniformitarianism is well-accepted. Critics have questioned whether
329 the use of the uniformitarian assumption is a form of “self-fulfilling prophecy” [83] that prevents the
330 possibility of identifying unusual or unrecorded demographic behaviour in the past, either because
331 prehistoric populations lived in environments that have no modern analogue, or because there is
332 greater variation across human biological and life history parameters than is frequently supposed,

333 particularly between Pleistocene and Holocene populations [84-85]. While this possibility cannot be
334 rejected outright, the null hypothesis should be that reconstructions of population dynamics and
335 structures should fall within the known envelope of human responses, at least when analysing *Homo*
336 *sapiens* populations. As life history parameters are subject to strong evolutionary constraints,
337 patterns of age-specific fertility and mortality, and their subsequent effects on population size and
338 dynamics, should vary in predictable, easily modelled, and fairly constrained ways [26].

339 Debate continues as to how far back in evolutionary and prehistoric time we can extrapolate human
340 demographic and life history parameters comparable to those of recent historical and contemporary
341 populations. The inapplicability of the assumption of demographic uniformitarianism in its strictest
342 form complicates palaeodemographic research into archaic hominin populations, even for the more
343 recent hominin species. Conversely, contradictions between expectations based on the
344 uniformitarian assumption and palaeodemographic data do not automatically mean that the
345 palaeodemographic data is best interpreted as representative of vastly different demographic
346 regimes; issues of sampling and poor preservation are even more pertinent in these stages of early
347 prehistory. The non-applicability of a strict principle of demographic uniformitarianism has far-
348 reaching implications for the study of the demography of archaic hominins across multiple
349 disciplines. It reduces the comparability of palaeodemographic data from archaic hominins—both in
350 terms of comparison with each other, and with *Homo sapiens*— even if derived using the same
351 method. It also means that greater caution must be taken in the use of values for absolute
352 population estimates and model parameters derived from recent populations to supplement the
353 prehistoric database, as the baseline justification for the use of these values is undermined.
354 Understanding the evolution of human life history traits, and their impact on the demography of
355 archaic hominins is one of the most important challenges of palaeodemography [26].

356 The principle of uniformitarianism features less heavily in areas of prehistoric demographic research
357 which focus on variables (such as population size and density) that are not directly subject to
358 uniformitarian principles, and which are usually interpreted in relative, rather than absolute, terms.
359 Nonetheless, as discussed in section 4, many palaeodemographic proxies contain assumptions about
360 factors such as mobility and social structure that are, in part, influenced by biology, life history, and
361 demographic parameters. In genetics, the estimation of effective or breeding population size from
362 patterns of genetic variation [86] requires an assumption of average generation length- an attribute
363 that likely varies between hominin species due to its relationship with life history parameters such as
364 age at first birth and rate of senescence. Although containing a cultural component, demography is,
365 at its core, the product of biological processes. The principle of biological and demographic

366 uniformitarianism that provides the theoretical scaffolding for palaeodemography should be borne
367 in mind by all who work in cross-disciplinary prehistoric demographic research.

368

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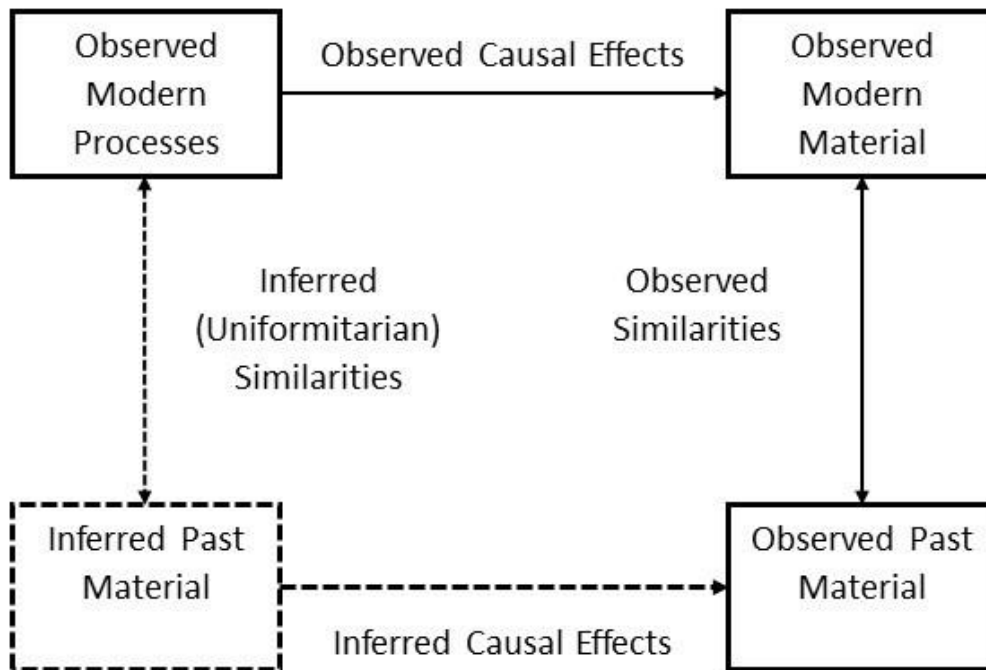
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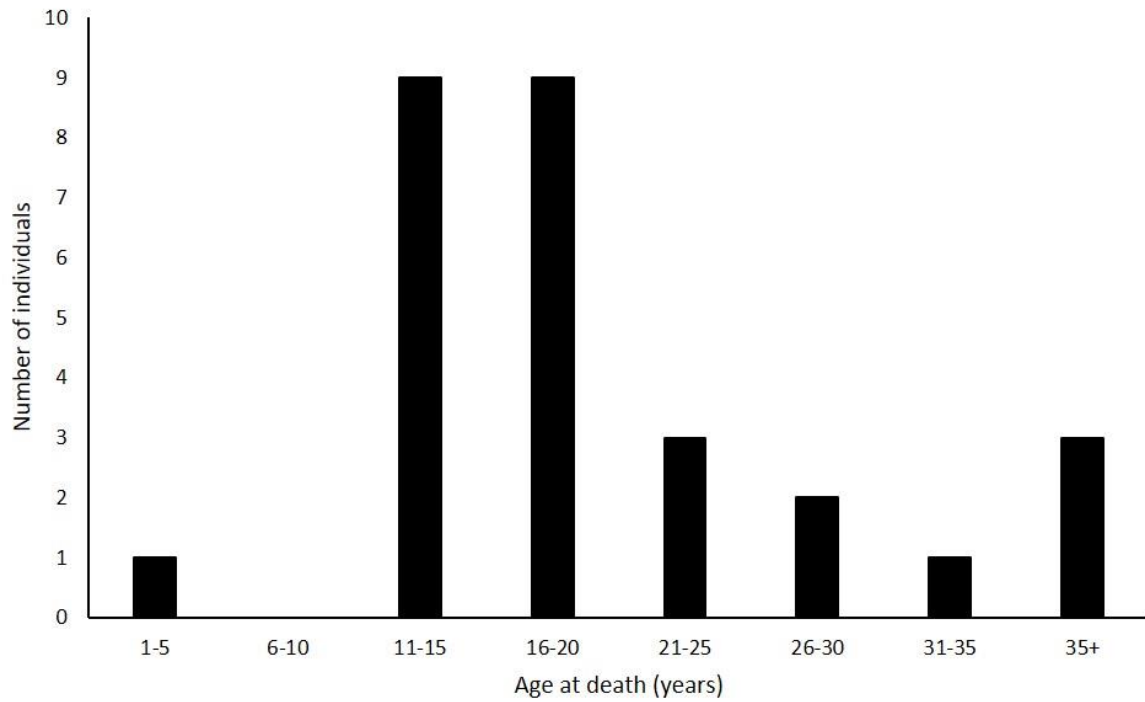
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684 **Figure 1.** Role of uniformitarianism in simple analogical reasoning. The uniformitarian principle
685 underpins the argument that similarities between modern and ancient materials can be explained by
686 inferring that unobservable past processes and their effects would have resembled processes
687 observable in the present day (after [6])
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700 **Figure 2.** The age-at-death distribution of the 28 Middle Pleistocene hominins from the site of Sima

701 de los Huesos, Spain. Redrawn from [61]

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